# AN INTERPRETATION OF THE MOLLUSCAN GENUS *AMPHIDESMA* IN NEW ZEALAND

By ELLIOT W. DAWSON.*

(Plate 4, text fig. 1-2.)

## SUMMARY.

*Amphidesma,* a genus of heterodont bivalve molluscs belonging to the Mactracea, is characteristic of the sandy beaches of New Zealand; it occurs in a similar habitat in Australia, Chile, Argentina, Brazil, and in a number of places in the Northern Hemisphere.

A history of the nomenclature of these molluscs, variously described as *Amphidesma* Lamarck, 1818, or as *Mesodesma* Deshayes, 1832, is given; it is concluded that *Donacilla,* based on De Blainville's publication of Lamarck's informal name of "Donacille," is the correct name to be used for this group of molluscs. The name *Amphidesma* (although a subjective synonym of *Semele* Schumacher, 1817) is being retained only for the purposes of the present paper.

A consideration of speciation within *Amphidesma* in New Zealand, from a morphometrical study of some 35,000 specimens, shows that a cline exists from northern New Zealand to the south with a gradual lessening in height to length ratios, and increase in length of posterior end to height and to length ratios with higher latitude. The ends of the cline are marked by the "typical" *A. subtriangulatum* and *A. forsterianum* in the north and south respectively. The cline is not simple since intermediate forms may be found in many otherwise uniform populations especially in the middle region of the cline embracing the southern part of the North Island and the northern part of the South Island, and also at the Chatham Islands. The development of these forms is correlated with events in the late Tertiary and early Pleistocene, especially with the influence of the warm East Australian Current, allowing immigration of the Peronian fauna to New Zealand and with the retreat and advance of Subantarctic waters over New Zealand in the late Pliocene.

The development of *Amphidesma* has been correlated with the marine biotic provinces of New Zealand. The north end-point of the cline is the "typical" *Amphidesma subtriangulatum* in the hydrologically stable subtropical Aupourian Province and the southern end-point with "typical" *A. forsterianum* in the hydrologically stable subantarctic Forsterian Province. The intermediate populations of mid-New Zealand and the Chatham Islands, showing great variability, lie in the hydrologically unstable Cookian and Moriorian Provinces where factors of larval dispersal have been so variable that the present populations clearly reflect these environmental conditions.

Three species of *Amphidesma* are found in New Zealand. *A. australe* (easily separable subgenerically as *Paphies*) and *A. ventricosum,* the Toheroa of commerce are both quite distinct. The third "species" is composed of a complex or group of populations regarded as variants of a polytypic species with the clearly marked end-points to which the names *A.*

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*Department of Zoology, University of Canterbury, New Zealand, and New Zealand Oceanographic Institute, D.S.I.R., Wellington.

*subtriangulatum* and *A. forsterianum* have been applied. The use of non-Linnaean "neutral terms" for informally describing these units is proposed.

The present account is offered as a preliminary to a major definitive revision of this genus now being undertaken.

## INTRODUCTION.

For a number of years it has been common practice to use the name *Amphidesma* to denote a genus of bivalve molluscs characteristic of many of the sandy beaches of Australia and New Zealand, and it is, indeed, the dominant mollusc of this particular habitat in New Zealand. These bivalves, belonging to the Order Heterodonta and preferably included in the Mactracea (although some authors place them among the Tellinacea), also occur on the coasts of Chile, Argentina, and Brazil, as well as some parts of the Northern Hemisphere, where, however, they do not appear to be so dominant on the sandy shore.

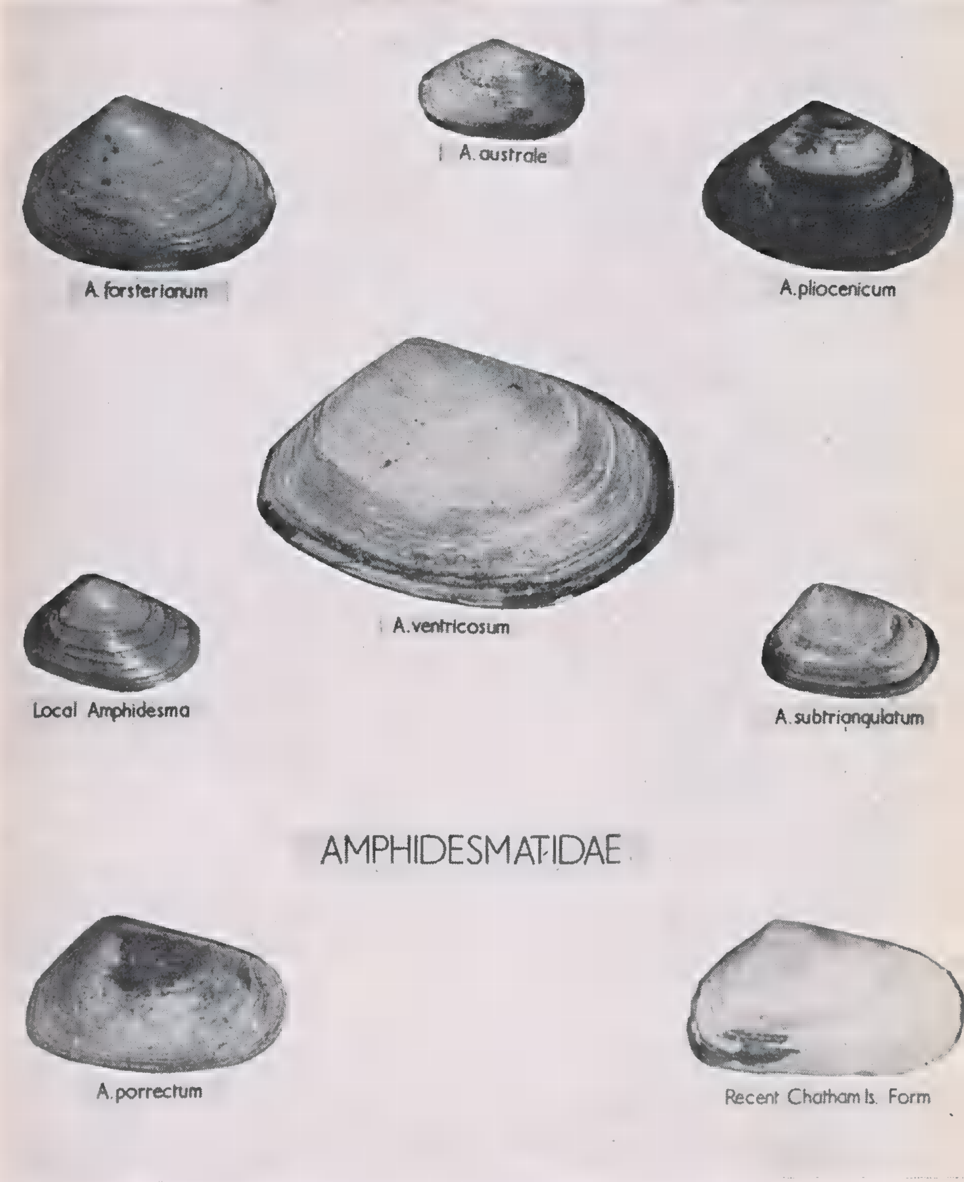
Powell's "Check List of the New Zealand Recent Mollusca" (various eds., 1937, 1946, 1957) uses the generic name of *Amphidesma,* and all recent discussions of these molluscs in New Zealand (*e.g.*) Fleming, 1951 b; Rapson, 1952, 1954; Cassie, 1951, 1955; Pilgrim, 1954 a, b; Owen, 1958; Morton, 1958) followed Powell's lead. In fact, after the discussions of this genus by Iredale (1915) and by Finlay (1927), the alternative name for the genus, that of "*Mesodesma,*" has not, despite Von Ihering's (1927) attempt to do so, been used in New Zealand since the time of Suter's "Manual" (1913), although many overseas workers have tended to favour it (*e.g.*, Prashad, 1932; Coen, 1933; Thiele, 1935; Viader, 1937; Gardner, 1943; Habe, 1952; Abbott, 1955; Soot-Ryen, 1959).

In Australia, *Amphidesma* seems to have been used for a long time by various authors for the faunas of all coastlines from Western Australia to the eastern States (Hedley, 1916, 1917, 1918), not only in systematic studies (Cotton and Godfrey, 1938), but also in recent distributional and ecological work (Kershaw, 1958; Stephenson, *et al.*, 1958).

Finlay's (1927) decision "to obviate further error" in identifying the species of *Amphidesma* and his acceptance of this generic name seem to have been taken as the "last word" by subsequent workers. But this use has not always found acceptance either in other works or in other parts of the world.

There is, and always has been, a great interest in the largest species in New Zealand, *Amphidesma ventricosum* (Gray, 1843), known as the Toheroa, which is marketed as a commercial product. The recently published work of Rapson and of Cassie has revealed something of the biology of this species which appears, both by morphology and by distribution, to be quite distinct to the malacologist. However, the other species found in New Zealand have been by no means always easy to identify, and this is one reason why the literature has become encumbered with various names of doubtful status and with various remarks of doubtful significance.

A study of the biology of the common species of *Amphidesma* living on the sandy shores of Pegasus Bay, on the South Island of New Zealand, was begun some years ago (Dawson, 1954). It was found that, before any progress could be made on studies of growth, distributions and



A. australe

A. forsterianum

A. pliocenicum

A. ventricosum

Local Amphidesma

A. subtriangulatum

AMPHIDESMATIDAE

A. porrectum

Recent Chatham Is. Form

PLATE 4.

relationships, the Pegasus Bay species must be certainly identified. Even from a cursory glance it did not appear to fall directly into any of the existing named species, and, accordingly, as a necessary preliminary to the biological work, an investigation into the systematics of the genus *Amphidesma* in New Zealand had to be undertaken.

During this investigation, samples were collected from every possible part of New Zealand and from the Chatham Islands, and this material was supplemented by that already existing in various museum collections. In only certain restricted areas, such as parts of the coastline north of Auckland, where, in any case, only one "typical" form seemed to be present, were there any serious gaps in this coverage. In all about 35,000 specimens were handled during this work, and of these some 23,000 were measured in several ways for statistical analysis. It must be added that these figures, although of an order adequate to give a fairly true idea of the variability of the species concerned, are not so impressive as might appear when considered in relation to the size of the beach populations being sampled. For example, it was estimated that, during the 1953-54 summer, a 20-mile stretch of Pegasus Bay carried a population of some 1770 million individuals; this compares favourably with Coe's (1953) estimate for the smaller *Donax gouldi* of *c.* 677,600,000 individuals along a five-mile stretch of beach in California.

The purpose of the present paper is twofold. In the first place, I want to present a preliminary statement of the history of the names "*Amphidesma*" and "*Mesodesma*" as applied to certain bivalve molluscs in the Australian and New Zealand regions, and to offer the conclusion that the name *Donacilla* only should be used for these "donaciform" bivalves living in this area or elsewhere, pending further evidence to the contrary based on other interpretations of the rules for the selection of type species.

Secondly, it is thought that an outline of the systematic position of the species of *Amphidesma* in New Zealand, and of their relationships, might be of interest to Australian workers, based on my 1953-1954 survey and pending the appearance of a definitive major revision of this genus which I am attempting. The major gaps in this treatment are the lack of comparative Australian and South American material and the fact that examination of the New Zealand fossil *Amphidesma* has not been completed.

In addition to this, the present account may, perhaps, stimulate others, who may have been interested in this genus, to examine the forms occurring in their own areas.

## 1. STATUS OF THE NAME *AMPHIDESMA*.

In 1818, Lamarck founded the genus *Amphidesma* to include sixteen species from various parts of the world. In proposing this genus, he explained:

"Depuis assez long tems, j'avais établi ce genre dans mes cours, sous le nom de donacille (extrait du cours, etc., p. 107), parce que l'espèce que je connus d'abord avait l'aspect d'une donace" (Lamarck, 1818: 490).

Lamarck himself thought that *Amphidesma* was an artificial group, but that it seemed to be united by a number of common characters.

Immediately following Lamarck's work of 1818, confusion began. Sowerby (1820) figured Lamarck's first species, *Amphidesma variegata,* but preferred to group the genus closer to *Mactra.* Latreille (1825) placed *Amphidesma* in a family of its own, closer to *Lyonsia* rather than to *Mactra,* while, amongst other authors, De Blainville (1824) placed *Amphidesma* in the existing genus *Lucina* containing, as he put it, "espèces lenticulaires ou ovulaires."

Dubois (1824: 49), in a free translation of Lamarck's work, stated: "La Marck, on his first examination of the species of this genus, called it Donacilla, considering them to be allied to those of the G. Donax; but, on a subsequent investigation, he has determined to constitute the present genus of them, as they possess very peculiar characters, and are quite distinct from all other bivalves."

It was evident to Deshayes that certain of the species put into *Amphidesma* by Lamarck were allied not only to each other, but to some other Lamarckian species outside this genus. Hence, in 1832, he founded the new genus *Mesodesma,* to which he transferred three species of Lamarck's *Amphidesma* (*A. donacilla, A. cornea,* and *A. glabrella*), and also Lamarck's *Mactra donacia* and *Crassatella striata.* No type species was mentioned by Deshayes for Lamarck's *Amphidesma* or for his own *Mesodesma,* although his *M. donacium* has been generally taken as such by later workers. Following the practice of delimitation of genera so favoured in the nineteenth century, the remaining species of Lamarck's *Amphidesma* were similarly transferred to other genera.

Reeve (1853), in his monograph on *Amphidesma,* remarked:

> "The genus as defined by Lamarck contained rather a miscellaneous assemblage of species. Some of these have been transferred to *Thracia,* some to *Mesodesma,* and some to *Syndosmya,* and several referred to this genus by Fleming and others have shared a similar fate. Of the Lamarckian species, *A. variegatum* (*Tellina obliqua,* Wood) may be regarded as the type of the genus as now constituted."

Lamy (1912 a: 159; 1914 a: 317) has outlined the fate of the sixteen Lamarckian species; briefly, five species now belong to *Scrobicularia* or to *Syndesmya,* three to *Mesodesma,* with one to each of the genera *Ervilia, Lyonsia, Thracia, Lucina, Thyasira, Lasaea,* and *Kellia.* In this way the genus *Amphidesma* has become an "empty shell." Nevertheless, the two gèneric names have been used and misused a great deal not only since the decision of Deshayes in 1832, but even since Lamy's reviews of the Lamarckian genera in 1912 and 1914.

Simply, the name *Amphidesma* seems to have been used for oblong, circular, or oval shells resembling *Semele* or *Syndesmya* or *Thracia* in appearance, while *Mesodesma* has, until quite recently, generally been applied to triangular or triangularly-ovate shells superficially resembling *Donax* or *Mactra.* Few workers have taken the trouble to look inside the shells and note details of ligament disposition, hinge and teeth as carefully as did Lamy in his studies of 1912 and 1914, and, hence, the names have often been used for quite superficial resemblances according to the whims of various writers.

We need not concern ourselves here with all the details and complications of the various species involved. Lamy's great reviews of the Scrobiculariidae, including *Amphidesma,* and of the Mesodesmatidae can be consulted by those interested in this aspect. But we can at once proceed to the basic question. What is the type species of *Amphidesma*?

Lamy (1912, 1914), with access to Lamarck's original material, decided in favour of his first listed species *A. variegatum*, and followed Deshayes in his use of the name *Mesodesma*. However, Iredale (1915), considering the same question at about the same time, selected, "by tautonymy," *A. donacilla*, the second listed species of Lamarck, and resurrected his genus *Amphidesma* for the benefit of conchologists in New Zealand and Australia. We may re-examine these choices now.

If the type species of *Amphidesma* should be found to be a "semeliform" shell, *Mesodesma* would be available as a later name for certain allied "donaciform" or "mactroid" molluscs regrouped and removed from the original genus by Deshayes in 1832. The "elimination" of this genus *Amphidesma* is, of course, quite contrary to modern taxonomic practice, since some consideration must be made of type species. In selecting the type species of *Amphidesma* by subsequent designation, we must accept the earliest type-designation, that of J. G. Children (1823: 301) who selected *A. variegata* Lamarck. This species, the first member of the genus listed by Lamarck, has been considered by several subsequent workers to belong to the genus *Semele* as *Semele purpurascens* (Gmelin, 1792), according to Lamy (1914 a:350), and listed earlier as *Tellina* or *Semele obliqua* (Wood, 1815) by Dall (1886:279) amongst others. Although it seems obvious that Lamarck founded his new genus on a specimen reminiscent of the genus *Donax* in shape and that he put forward the name *Amphidesma* as a proper substitute for the vernacular "donacille," there seems to be little doubt that *Amphidesma* must be based on a "semeliform" rather than a "donaciform" animal other characters as portrayed by Lamarck being equal. Sowerby's (1820) figure of *A. variegatum* certainly indicates a "semeliform" species.

Since *Amphidesma*, based on a semeliform animal, is considered a subjective synonym of *Semele*, the "donaciform" members of the genus, separated by Deshayes, can now bear the name "*Mesodesma*." However, the name *Donacilla*, the Latinised version of Lamarck's "donacille" of 1812 has priority since it was first published, as Iredale (1915:490) has already shown, by De Blainville (1819:428):

> "DONACILLE, *Donacilla*. (Conchyl.) M. de Lamarck, dans l'extrait de son cours, etc., page 107, avait donné ce nom de genre á une coquille bivalve, ayant l'aspect d'une donace, qu'il a fait entrer depuis dans le genre qu'il a nommé Amphidesme. Hist. nat. des anim. sans vert., 2ᵉ édit., t. 5, p. 489 (De B.)."

Dr. L. R. Cox, F.R.S., has kindly drawn my attention to this question of priority, and has given me his opinion on the procedure necessary, and I am accordingly greatly indebted to him.

It seems that *Donacilla* must be treated as a generic name published with an indication but without an included nominal species, so that the first nominal species included in *Donacilla* becomes its type. The first author to adopt the generic name *Donacilla* Lamarck and to associate a nominal species with it was R. A. Philippi (1836:37, see also 1853:305, 311), who described a new species as *Donacilla lamarckii* and placed in its synonymy *Mactra cornea* Poli and *Amphidesma donacilla* Lamarck. This enables the adoption of the generic name *Donacilla* for the "donaciform" members of "*Amphidesma*" and for those of Lamarck's genera which were removed to "*Mesodesma*" by Deshayes. If "*Mactra donacia* Lamarck," the type of *Mesodesma,* is considered as congeneric with the type species of *Donacilla, i.e., Amphidesma donacilla,* then only *Donacilla* is available for this group, and, in any case, it must be considered as validly published prior to *Mesodesma.* A fuller treatment of this particular section of the present paper is being offered elsewhere (Dawson, 1959).

## 2. THE NEW ZEALAND SPECIES OF AMPHIDESMA.

Iredale (1915) has, in detail, set out the history of early changes in the nomenclature of *Amphidesma,* and this account is expanded and criticised by Finlay (1927). Oliver's work (1923) was apparently lightly dismissed by Finlay, but, as may appear from the present study, it is possibly the closest and most clearly outlined description of the status of this genus in New Zealand.

It is not necessary here to quote extensive synonymy nor to delve deeply into the history of the genus, but the salient features may be mentioned. Deshayes (1832) had included the following presumed New Zealand species in his genus *Mesodesma*: *M. donacium* ex Lamarck, *M. quoyi sp. nov.* and *M. gaymardi sp. nov.* Dall (1895; 1898) divided "*Mesodesma*" into the subgenera *Mesodesma, Donacilla, Taria* and *Paphies,* and Suter (1913) in his great "Manual of New Zealand Mollusca" followed Dall's usage and listed the New Zealand species thus: *Mesodesma* (*Donacilla*) *subtriangulatum* (Gray, 1825), *M.* (*Taria*) *ventricosum* Gray, 1843, and *M.* (*Paphies*) *australe* (Gmelin, 1791). A key to these subgenera was also given by Suter.

Iredale's (1915) interpretation of the New Zealand species was: *Amphidesma* (*Taria*) *gaymardi* (Deshayes, 1832), *A.* (*Taria*) *quoyi* (Deshayes, 1832), *A.* (*Taria*) *ventricosum* (Gray, 1843), and *A.* (*Paphies*) *australe* (Gmelin, 1791). Looking further into the species listed by Iredale, we find that, for a number of reasons, he regarded *A. gaymardi* as the name to be used for the species included by Suter as M. *subtriangulatum* (Gray, 1825). Iredale associated this species and *A. ventricosum* in the subgenus *Taria,* as there did not appear to be much superficial distinction, and he noted that the pallial sinus was small in both *A. gaymardi* and *A. quoyi,* but deep in *A. ventricosum.* Iredale considered that Suter had confused *A. quoyi* in his description of *M. ventricosum.* Furthermore, Iredale distinguished *A. quoyi* from *A. ventricosum* in the following points: "*A. ventricosum* Gray is longer and narrower than *A. quoyi* Deshayes, and approaches *A. gaimardi [sic]* in shape. *A. quoyi* has the posterior slope flattened, while in *A. ventricosum* the posterior slope is bicarinate. In *A. quoyi* Deshayes the siphonal inflection is not deep whilst in *A. ventricosum* Gray it is very deep." Suter, in his description of *M. ventricosum,* stated that the pallial sinus is horizontal with a circular anterior end reaching not quite the middle of the shell, and he made no mention of a bicarinate posterior end. However, in his description of the subgenus *Taria,* in which he placed *M. ventricosum,* he noted: "pallial sinus well marked, sometimes deep." Hence, both of Iredale's species *A. quoyi* and *A. ventricosum* could be included in this subgenus *Taria.*

Oliver (1923) discussed the nature of *A. subtriangulatum*, and his remarks, as earlier mentioned, are worthy of some attention. He said of this species: "This appears to be a variable species, the extreme forms of which are the thick, angled, triangular form from the North, and the flattened, more ovate, form from Banks Peninsula and other localities to the South." He pointed out that, contrary to Iredale's notions, Suter had not confused *A. quoyi*, which was represented by these southern more ovate shells, with *A. ventricosum*, but had included it in his description of *A. subtriangulatum* by the use of a series probably greater than was available to Iredale. Oliver continued, interestingly, thus:

> "That we are dealing with one variable species, and not two species, is shown by the fact that variations in those characters which are supposed to separate *quoyi* from *subtriangulata* may be observed in the same locality. For instance, in shells from the Chatham Islands the angle formed by the dorsal and posterior side varies through several degrees, while shells from Takapuna vary in the thickness of the shell. While it is thus not practicable to separate a long series of shells from many localities into two species, yet those from the north-east coast between Spirits Bay and Tauranga are usually heavy ventricose shells with the posterior end short and, therefore, the angle made by the dorsal and posterior sides comparatively small. Shells from Kaipara and Gisborne southwards, and from the Chatham Islands, are almost invariably of the broad-angled, thin form. If it be convenient to refer to these differences *subtriangulata* and *quoyi* might be used subspecifically, but in this case *quoyi* would not have the meaning intended by Iredale, but include besides the greater part, so far as area of distribution goes, of the species *subtriangulata*."

Finlay (1927) attempted to end all confusion as to the species of *Amphidesma* in New Zealand. He began his criticisms by stating that Oliver's notes needed some revision since he had confounded distinct species. Oliver had, according to Finlay, misinterpreted Iredale's comments on Suter's identification of *M. quoyi* with *M. ventricosum*, and Finlay emphasised Suter's use of the expression "pallial sinus well marked, sometimes deep" in his description of the subgenus *Taria*. Finlay stated that the pallial sinus in true *ventricosum* is always deep and "so that only one conclusion is possible to account for the use of the word "sometimes," and that is that a species with a short pallial sinus had also been examined." However, one may now note that, in Suter's key to subgenera, *Taria* is characterised by the possession of a pallial sinus "reaching to near the centre" and, therefore, Oliver's suggestions, based on Suter's actual specimens and on Suter's inclusion of *M. lata* as a synonym, that *quoyi* was included by Suter in his *M. subtriangulatum* are apparently substantiated. Finlay further pointed out that one cannot adopt Oliver's suggestion of using the names "*quoyi*" and "*gaymardi*" subspecifically since both these names, and *subtriangulatum*, were given to the northern forms as is shown from a study of such published figures as are available. Finlay found, therefore, that the southern, more ovate, form was nameless, a point which concerns the species from Pegasus Bay which forms the basis of the present study. The confusion, he suggested, was due to the fact that there are two bicarinate species, *i.e., subtriangulatum* is bicarinate as well as *ventricosum*, whereas the southern shell is smooth, having no carinae on the posterior margin. Finlay's conclusion was that ". . . we can now understand how *subtriangulatum* was sometimes lumped with the southern shell (on account of its shape and sinus), and sometimes, by Suter, with *ventricosa* (on account of its two carinae) . . .”

Finally, Finlay proposed the name “*Amphidesma forsteriana*” for this southern species. The key he gave, which implied the “last word” on the *Amphidesma* question, is given again here:

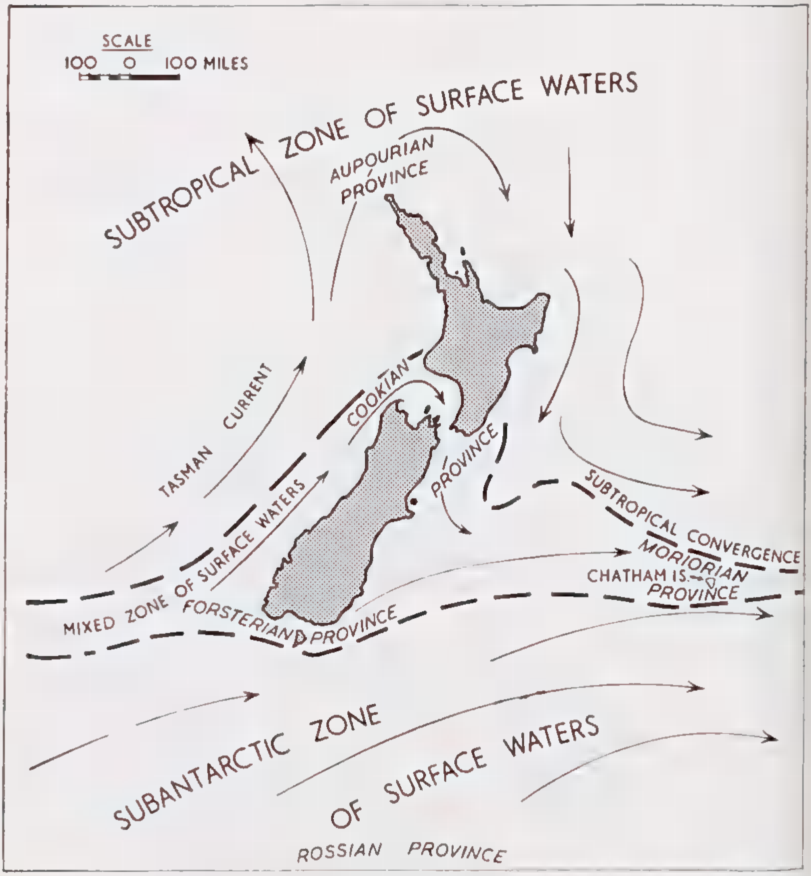
| | |
|---|---|
| “Shell inequilateral | |
| Adult shell posteriorly bicarinate. | |
| Pallial sinus deep | *ventricosa* |
| Pallial sinus shallow | *subtriangulata* |
| Adult shell posteriorly unicarinate, sinus shallow. | |
| Shell very high and crass, posterior dorsal area cut straight in | *crassiformis* |
| Shell high but not crass, posterior dorsal area moderately cut in | *pliocenica* |
| Shell neither high nor crass, posterior dorsal area rather expanded | *forsteriana* n. sp. |
| Shell subequilateral, not carinated | *australis.*” |

This key, since it represents the latest opinion on the New Zealand species, may be taken as the starting point for the present inquiry.

The *Amphidesma* in Pegasus Bay, the Banks Peninsula populations and those from Otago beaches all seem to fall into Finlay's *A. forsterianum* which he characterised as having an “inequilateral rather small shell not high nor crass, nor inflated; rather short anterior end in comparison with *subtriangulata,* and more produced posterior end, the beaks being therefore much less posterior; wing-like expanded posterior dorsal area, not sharply cut in, and with no distinct second medial carination, the bordering main carination being itself weak; and short pallial sinus.”

On passing up the South Island into the Cook Strait region and along the Wellington coasts, we find shells appearing with characters of shape between the two extremes of *A. subtriangulatum* (= “*subtriangulata*” of Oliver) and *A. forsterianum* (= “*quoyi*” of Oliver). The Toheroa, *A. ventricosum,* is a distinct enough form although the representatives from the Southland beaches appear to be more truncated anteriorly and may, as Finlay suggested, deserve taxonomic recognition. The very small individuals of *A. ventricosum* and *A. subtriangulatum* are often rather difficult to distinguish in the field. On the Chatham Islands, 500 miles to the east of Banks Peninsula, shells occur which seem to have what might be called “*subtriangulatum* tendencies,” although others appear to belong to *A. forsterianum* with populations resembling the fossil form *A. porrectum.* It is of interest, in this connection, to note Finlay's (1928: 280) remarks: “It would be very interesting if the broad, triangularly ovate, unicarinate *forsteriana* Finlay were to occur at the Chathams also, as this would prove the two forms absolutely distinct, instead of only regional relatives. Till evidence is forthcoming, however, it seems best to admit only *subtriangulata* to the Chathams fauna.” A second quite distinct medial carination has sometimes been seen in “typical” *A. forsterianum* from Banks Peninsula and Otago, and in many others the bordering main carination of the posterior dorsal area is quite angled. The pallial sinus in both northern and southern forms appears similar in size, shape and position, although individual variation exists, as may be seen by glancing at the shells forming any single natural population.

Lack of precision of the delimitation of the various forms is such that both the figure of *A. subtriangulatum* given by Suter (1915, pl. 59, fig. 19) and by Powell (1937, pl. 11, fig. 7) may be taken as representing examples of the intermediate forms rather than the "typical" forms. However, Moss (1908, pl. 8, fig. 24) illustrated, under the name of *Atactodea subtriangulata*, a "typical" example of *A. subtriangulatum*. Bucknill's figure (1924, pl. 17, fig. 13) illustrates a shell close to the "typical" *subtriangulatum*. Indeed, Powell's figure could well illustrate some of the Chatham Island shells, in particular specimens which I collected in 1954 from Ko-ro-Kopuroa, near Owenga.



Text Fig. 1.

Of extinct species of *Amphidesma,* several have been collected in New Zealand. *A. crassiforme,* described by Marshall and Murdoch (1920) on three valves from blue sandy clay at Nukumaru (lower Pleistocene), was "distinguished by its massiveness and abrupt heavy truncation." *A. porrectum,* described by Marwick (1928) from mid to upper Pliocene soft Bryozoan limestone at Titirangi, Chatham Islands, was "distinguished from *A. subtriangulatum* by the greatly elongated anterior end, and the generally strongly convex posterior end, also the pallial sinus is deeper and the posterior muscle scar somewhat larger." Many further specimens of this form were collected in 1954 at the type locality for the present study. *A. subtriangulatum pliocenicum,* described by Oliver (1923: 187) from "the Pliocene beds at Castlecliff" (now regarded as Pleistocene), was distinguished by being "higher than either of the recent forms, and the angle of the dorsal and posterior sides is intermediate. It is more distinct from the two recent forms than they are from each other . . ." Oliver's last remark, as first pointed out by Finlay (1927), is belied by the fact that, in general, *pliocenicum* possesses no secondary carination, and it seems to be directly ancestral and quite close to *A. forsterianum.* Dell (1950) has described from a single valve an early *Amphidesma* from a Miocene bed at Waikiwhai, Auckland, as *A.* (*Paphies*) *anteaustrale.* Recent species occurring as fossils, distinguished earlier as separate species in many cases but now synonymised, have been listed by Hutton (1873, 1880), Suter (1910, 1918), and Thomson (1920), and Te Punga (1952). Finlay (1924) has listed from the Miocene of Awamoa a young shell considered to be "*Amphidesma subtriangulatum* Wood" found in very hard and rather poorly fossiliferous mudstones, now regarded as of upper Pliocene date. Finlay suggested that this shell might be "referable to the subsp. *pliocenica* Oliver." Apart from Dell's record of *Amphidesma* (*Paphies*) from the lower Miocene (Altonian), this may well be the earliest record of the genus in New Zealand if it is authentic. Dr. J. Marwick (pers. comm., 1953) has been unable to locate this specimen in the Geological Survey collections.

## 3. SPECIATION WITHIN AMPHIDESMA.

For the purposes of the present paper aspects of speciation and distribution of *Amphidesma* will be discussed only in general terms. Extensive data, in the form of specimens and measurements, is, however, available to substantiate statements which may be made here.

*Amphidesma,* although of little value to the palaeontologist concerned with happenings in the Tertiary, is a useful genus in two ways: it illustrates the variation that may occur within a single genus in recent times, and, secondly, it is a convenient model for demonstrating the status of the concept of marine biotic provinces within New Zealand.

The nature of "species" has been well dealt with on a number of occasions by Mayr (1942, 1948, 1957), and, for the palaeontologist, by Sylvester-Bradley and others (1956). Mayr has shown that, basically, there are only two species definitions: "morphological," based on the degree of difference, and "biological," based on the amount of gene interchange—in other words, on the degree of reproductive isolation. Mayr's (1942) definition of species as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" may be commended as a simple expression based on the population, *i.e.,* on the smallest interbreeding unit.

It appears well founded, from earlier authors' conclusions and from a consideration of the present distribution of *Amphidesma,* that there are, in New Zealand, three living "species," *A. australe, A. ventricosum* and the *A. "subtriangulatum–forsterianum" group.*. It is in the consideration of the extent and limits of this third "species" group that difficulties arise. It can be shown by examination of the ratios of length of posterior end to height (D/H) and of length of posterior end to total length (D/L) for populations of *Amphidesma* from throughout New Zealand that an apparent cline (see also, Clench, 1954) may exist in which there occurs a gradual morphometric character change with latitude. As *Amphidesma* progresses from northern New Zealand south towards Stewart Island, there is a gradual lessening of the height to length (H/L) ratio, an increase in D/H and D/L and, hence, a prolongation and expansion of the posterior end with higher latitude. The ends of the cline are marked by the "typical" *subtriangulatum* and *forsterianum* forms. This cline is not so simple, however, as it may appear. Intermediate forms may be found in many otherwise homogeneous populations. This is particularly so in the region embracing the southern part of the North Island and the northern part of the South Island and also at the Chatham Islands. Infraspecific categories have always proved a headache for taxonomists, both with recent (Mayr, 1942, 1957; Emerson, 1952), and with fossil material (Newell, 1947: Dawson, 1952; Sylvester-Bradley, *et al.,* 1956). Mayr (1942) defined the only recognised infraspecific category, the subspecies, thus: "Subspecies are geographically defined aggregates of local populations which differ taxonomically from other such subdivisions of a species." Subspecies must be considered, also, as an assemblage of local populations. Such populations are classified on these bases: geographical relationship, presence or absence of morphological difference, and of reproductive isolation.

Perhaps the populations of *Amphidesma* in the intermediate zone of this supposed cline might be thought of as marking the area of contact of two well-defined subspecies. The morphological characters of expansion of posterior end and, particularly, presence of carinae or rays do not seem to be strictly valid for designating each population, and almost every local group appears "different," so that shells may be referred to certain beaches merely by examination of the external morphology.

Despite this, instead of taking the "easy" way out and merely calling each "different" group a new species or subspecies, it seems possible to reconcile this variation with the late geological history of the New Zealand marine molluscs. Fleming (1944) and Dell (1952) have outlined the general distribution of ocean currents in relation to New Zealand. Without going into details of the oceanography involved, it may be said that a warm current from eastern Australia, the "Notonectian Current" (= East Australian or Tasman Current) strikes New Zealand in the vicinity of South Westland and travels the length of the West Coast, joining up with other water movements from the South-west Pacific to form the East Cape Current, sometimes sweeping well down to Banks Peninsula or further south during the summer. On the other hand, the cold West Wind Drift, from the Subantarctic, also approaches the South Island, sweeping eastwards towards the Chatham

Islands. In this way, a zone of so-called "mixed" waters is formed. The boundary, approximate as it may be, between the "warm" and "cold" waters, is referred to as the Subtropical Convergence, and profound influences on faunal relations have been correlated with it.

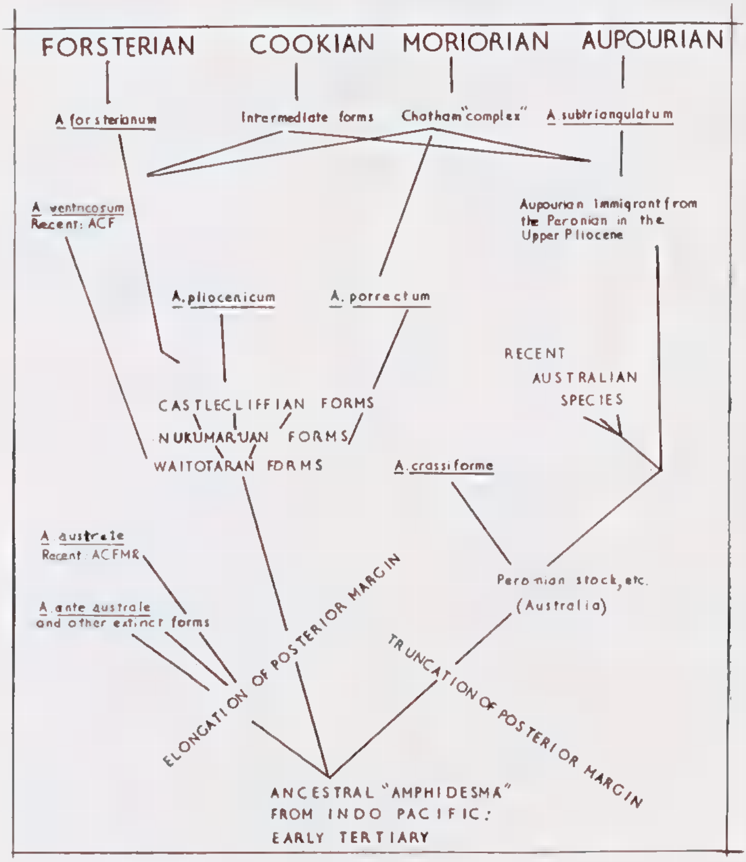
The development of the New Zealand molluscan fauna seems to have been such that, as Fleming (1944, 1949, 1951 a) has shown, several trends may be noted: (1) the evolution of an "autochthonous" element, the ancestors of which were already on the New Zealand scene in early Tertiary or even late Cretaceous times, (2) the reinforcement of such fauna by Indo-Pacific and possibly other elements during the Tertiary, (3) the extinction of mid-Tertiary genera in the Miocene and early Pliocene, and (4) the sudden immigration of species of East Australian origin in the late Pliocene and early Pleistocene, which has continued in post-Pleistocene times.

*Amphidesma,* in New Zealand, may be considered to appear in the Waitotaran Stage of the Upper Pliocene and in the Lower Nukumaruan Stage of the lower Pleistocene. Conditions, then, were such that there was a northward advance of cold water accompanied by migration of a number of genera of southern origin into what is now the middle of New Zealand. In this way, areas in North Canterbury, southern Hawke's Bay, and Wanganui, were affected by seas of the Subantarctic zone. In the Upper Nukumaruan, a retreat took place. *Amphidesma* may have become established in these times and some of the "odd" fossil forms, about which little data are available, may be correlated with happenings at this time. In the following stage of the Pleistocene, the Castlecliffian, the influence of the Tasman Current was felt, many genera from the east Australian sources now having suddenly appeared. This is, no doubt, when *Amphidesma,* as such, became an obvious faunal element, since additional stock may have been brought in from East Australia. The presence of the Tasman Current inhibited further advance of Subantarctic waters and prevented New Zealand seas from showing the further effects of cooling which culminated in the Pleistocene glaciation.

*Amphidesma "forsterianum"* may be considered the recent expression of late Pliocene stock. Nukumaruan specimens suggest that the ancestral *Amphidesma,* as indicated in *A. pliocenicum* of Oliver, was of a high H/L ratio with an elongated and expanded posterior end. The hypothesis is offered here that this group of forms, gradually evolving in early Pliocene times, retreated southwards with the Notonectian influence. The Castlecliffian immigration, with the new stock of *Amphidesma,* contributed further variation and, particularly in North Auckland, *Amphidesma* of another form, with a truncated posterior end and a more massive shell, occurred, perhaps as a direct result of the immigration of Peronian fauna from East Australia or as a descendant of the fossil *A. crassiforme.* It is further suggested that, in later time, the *"forsterianum"* stock gradually moved northwards again and the *"subtriangulatum"* or Peronian stock moved southwards, a trend which may well be continuing. In another connection, it has already been shown (Dawson, 1952) with reference to changing conditions in the New Zealand climate what rapid evolution may occur in small isolated communities. The limiting factor preventing further intermixing of surface waters and dispersal of larvae from various stocks may be principally one of temperature associated with general hydrology (cf. Fleming, 1952). At this point we may conclude this account by associating developments within *Amphidesma* with present concepts of marine faunal provinces in New Zealand.

## 4. DISTRIBUTION OF *AMPHIDESMA* IN RELATION TO MARINE BIOTIC PROVINCES IN NEW ZEALAND.

The division of the New Zealand (or Maorian) sub-region into faunal provinces, a province being an area within a faunal region exhibiting a marked percentage of endemism, was the result of the efforts of Iredale, Finlay, and Powell. Hydrologically, the provinces may be delimited thus: AUPOURIAN—within the Subtropical zone of surface water—North Auckland peninsula and the Three Kings Islands from above Ahipara on the west Auckland coast and Whangaroa on the east coast; COOKIAN—mixed waters of the middle region of New Zealand—rest of the North Island and the northern part of the South Island south to Westport on the west coast and Banks Peninsula on the east coast; FORSTERIAN—isolation and predominant Subantarctic waters—Otago, Southland and Stewart Island; MORIORIAN—isolation and mixed waters—the Chatham Islands; ROSSIAN—completely within the Subantarctic zone of surface water, Subantarctic islands and seas.



Text Fig. 2.

The Aupourian province seems, indeed, to be the domain of the "typical" *Amphidesma subtriangulatum*, the northern end of the so-called cline. Almost all marine organisms found in this province are characteristic of Subtropical conditions, and hence *A. subtriangulatum* here may be stenozonal, being limited by temperature considerations. On the other hand, the Forsterian province is clearly defined for most molluscs as a predominantly Subantarctic zone and is none the less so for *Amphidesma*, this being the domain of the "typical" *A. forsterianum*.

The particularly interesting provinces, from the aspect of *Amphidesma* and the dispersal of its larvae, are the Cookian and the Moriorian. The Cookian, as indicated, is within a zone of relatively mixed waters. The fluctuation in position of the Subtropical Convergence, which may be considered its northern boundary, makes this zone hydrologically unstable and hence biologically variable. Hence it is not surprising that within this zone *Amphidesma* should show great variation. It is only from Westport, on the west coast of the South Island, and from Pegasus Bay, on the east coast, that *Amphidesma* appears morphometrically stable to the south. In the north, it seems that only from about Kawhia and Tauranga, on the west and east coasts, respectively, of the North Island, does this occur, although *Amphidesma* with "*forsterian*" affinities occurs even at Manukau Heads, near Auckland.

## CONCLUSIONS.

It can be seen that *Amphidesma* is a highly variable genus in New Zealand, and some doubt may be expressed as to a suitable nomenclature for the various forms, along the lines proposed by Newell (1947) or by Emerson (1952).

*Amphidesma subtriangulatum pliocenicum*, so named by Oliver, appears close to the recent *A. forsterianum* of Finlay, and much more distantly related to the Aupourian "typical" *A. subtriangulatum*. Hence, it might be suggested that the fossil form be raised to specific rank and, thus, that *A. forsterianum* = *A. pliocenicum*. However, since *A. subtriangulatum, sensu stricto*, is not clearly separable from the Recent Cookian *Amphidesma*, then, perhaps, the wisest thought would be to regard all these forms as variants of a polytypic species:

| | |
|---|---|
| Aupourian, | *A. subtriangulatum subtriangulatum;* |
| Cookian, | *A. subtriangulatum cookianum;* |
| Forsterian, | *A. subtriangulatum pliocenicum;* |
| Moriorian, | *A. subtriangulatum moriorium.* |

Systematics, as such, is useful to the ecologist for practical purposes since it enables him to have a "label" by which to refer to the particular animals with which he is dealing. As his studies become more refined, a mere label is not enough, and he will need to know precisely with which animal he is dealing and something of its relationship to other similar animals. Within the gross limits of the working needs of marine ecologists in New Zealand the above scheme may be useful until the full details of the complexes and intermediate forms, such as occur in the Moriorian and Cookian provinces due to the interplay of larval disperdal and hydrology, are made clear.

Convenient expressions, known as "neutral terms," are available for informally describing taxonomic units of doubtful status. The terms generally used are *form*, for a single unit, and *group* or *complex*, for a number of units. Hence, form may be used when it is not known whether the unit being considered is a full species, a subspecies of a polytypic species, or merely an individual variant. The taxonomic status of the molluscs belonging to the genus *Amphidesma* in New Zealand may be resolved in the following way: *A. ventricosum* is predominantly Aupourian, extending into the Cookian with a representative, possibly the mark of a relict fauna, in the Forsterian. *A. australe* (conveniently separated subgenerically as *Paphies*) is euryzonal, extending from the Aupourian to the Forsterian and Moriorian, with a representative in the Rossian (= Antipodean). In contrast to these relatively clearly defined species, there is what may be called the *Amphidesma subtriangulatum* Group or Complex. Since a non-Linnaean terminology is to be preferred, the varieties found in each marine province may be referred to as the Apourian Form, the Cookian Form, and the Forsterian Form, with the mixed populations of the Chatham Islands, where the situation seems especially involved, known as the Moriorian Complex.

Finally, *Amphidesma*, as a taxonomic problem, has well illustrated the change in thought of systematists within the past fifty years from the "type" concept of the nineteenth century conchologist to the "population" concept of Mayr, Dobzhansky, Simpson, and Huxley. In New Zealand, and also in Australia, it appears that the "new" systematics is yet to fill its role fully, and, while agreeing with Dell (1953) that we must bewail the state of affairs that results from "a constant search for differences, forgetting the likenesses, from a desire to name all separable forms and from a lack of appreciation of the facts of geographical variation and isolation," it is felt that the further delimitation and intensive study of populations of such variable genera as *Amphidesma* will prove invaluable in putting molluscan systematics in New Zealand, and in Australia, on a sound basis. Apart from this, it is suggested, based on the idea expressed in Occam's Razor that hypotheses should not be unnecessarily increased in number and should be phrased in the simplest possible way, that to call a "different" form a *new* species is, in these days of enlightened taxonomic thought, not sufficient, and evidence must be brought forward to show how otherwise it could not be filled into the existing framework of that particular genus or unit.

I should like to conclude by expressing my appreciation of the guidance and friendship of the late Professor E. Percival, F.R.S.N.Z., University of Canterbury, New Zealand.

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